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Seasonal changes in the respiratory electron transport system (ETS) and respiration of the zebra mussel, *Dreissena polymorpha* in Saginaw Bay, Lake Hnron

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Abstract

Electron transport system activity (ETS) and respiration rates (R) of the zebra mussel, *Dreissena polymorpha*, were determined monthly from April to November over 2 years at two sites in Saginaw Bay, Lake Huron. The sites were located in the inner and outer bay and contrasted in food quantity and quality. ETS ranged from 2 to 40 μg O_2 mg DW^{-1} h^{-1} over the study period. Both ETS and respiration were strongly related to temperature, and maximum values were found between June and August. ETS also peaked in June/July when assays were conducted at a constant temperature (25 °C), indicating other factors besides temperature affected metabolic activity. R:ETS ratios decreased with increased temperature at the inner bay site, but trends were minimal at the outer bay site. In late summer, blooms of the cyanophyte *Microcystis* occurred in the inner bay, likely depressing filtration rates, and leading to lower respiration rates relative to ETS. ETS activity was consistently higher in the outer bay and was likely a result of higher food quality. Despite these spatial differences, annual mean R:ETS ratios varied only from 0.04 to 0.09 at the two sites over the 2-year period. Based on these values, ETS may be useful as an indicator of long-term metabolic activity in annual energy budgets of *D. polymorpha*. However, food conditions differentially affect respiration relative to ETS, and variability in this ratio must be considered when interested in shorter time scales.

Introduction

The introduction and rapid expansion of *Dreissena polymorpha* (zebra mussel) in North America has led to broad ecological changes in many lake and river systems (MacIsaac, 1996; Strayer et al., 1999; Nalepa et al., 1999). With high filtering rates and often great abundances, *D. polymorpha* populations alter normal energy flow patterns and cause cascading changes throughout the aquatic food web. In turn, the population responds to created changes until the population is at equilibrium with the surrounding environment. To this extent, understanding population dynamics relative to environmental variables is critical to predicting eventual population size. Population energy budgets are useful in this regard since the energy used for population growth can be defined relative to energy needed for population maintenance (Schneider, 1992; Stoeckman & Garton, 1997). Components of an energy budget for *D. polymorpha* such as consumption, somatic growth, fecundity and metabolic costs (respiration, excretion) have been examined under different environmental regimes (mostly food and temperature) in both the field and laboratory (Walz, 1978a, b, c; Sprung, 1995a, b, c).

Of the various budget components, respiration is often the dominant consumptive pathway of ingested organic material. For instance, an energy budget for *D. polymorpha* in western Lake Erie indicated that respiration alone accounted for 88% of caloric

intake (Stoeckman & Garton, 1997). Despite its importance, however, respiration rates are generally determined in the laboratory where unnatural conditions and short-term stress can lead to inaccurate rate measures (for summary see Cammen et al., 1990). While such laboratory-collected data may be useful for determining relative response to manipulated environmental variables, or for assessing comparative metabolic physiology, results may be limited in scope and unrealistic when applied to assessments of population energetics under field conditions.

In this paper, we examine the use of the electron transport system activity (ETS) to estimate *in situ* metabolic rates of *D. polymorpha* in Saginaw Bay, Lake Huron. Our purposes were to document relative ETS activity and respiration rates under natural conditions, and to examine environmental factors that may affect this relationship over a seasonal period. By definition, ETS consists of a complex chain of macroenzymes (cytochromes, flavoproteins, metalic ions) in cell mitochondria that transport electrons from catabolized food materials to oxygen. Since the synthesis and degradation of these macroenzymes is a function of the respiratory requirements of the organism, measurement of enzyme activity provides a time averaged value of the maximum oxygen uptake rate potential. Since an organism's ETS activity requires several days to weeks to adjust to changes in environmental conditions, it is less subject to experimental artifacts and short-term fluctuations when compared to direct measurements of respiration (Bamstedt, 1980; Cammen et al., 1990).

The assay for ETS activity estimates the potential respiratory capacity of the organism by measuring the enzymatic activity of the rate limiting step in oxygen utilization for adenosine triphosphate (ATP) production. For ETS, this step is the oxidation of the coenzyme UQ-cytochrome b complex (Broberg, 1985). The assay has been widely used to measure the oxygen consumption potential of seawater, sediments, phytoplankton and zooplankton (Packard, 1971; Packard et al., 1971; Jones & Simon, 1979). While Cammen et al. (1990) used ETS to examine metabolic activity in several marine species of benthic macroinvertebrates, the technique has not yet been generally applied to freshwater benthic forms. Recently, Madon et al. (1998) conducted laboratory studies to evaluate factors affecting ETS and respiration rates in *D. polymorpha*. The relationship between ETS activity and respiration was unaffected by mussel size and food ration, which prompted the authors to suggest that ETS may be a reliable predictor of *D. polymorpha* respiration under natural conditions. We further examine the use of ETS to estimate the metabolic activity in *D. polymorpha* by comparing ETS and respiration rates over two seasonal periods at two sites of varying trophic status.

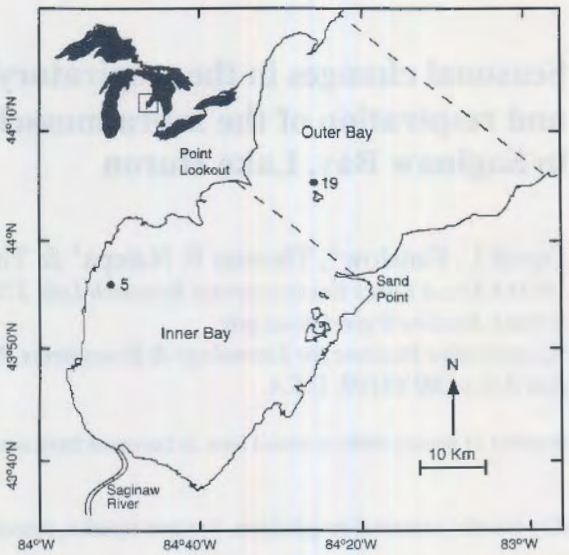

Figure 1. Sampling sites in Saginaw Bay, Lake Huron where *D. polymorpha* was collected for determination of ETS activity and respiration rates in 1995 and 1996.

Materials and methods

Description of study site

This study was conducted in Saginaw Bay, which is a shallow, well-mixed extension of the western shoreline of Lake Huron (Fig. 1). Based on differences in physical and chemical features (Beeton et al., 1967; Smith et al., 1977; Johengen et al., 1995), the bay can be divided into an inner and outer region by a line extending along its narrowest width from Sand Point to Point Lookout (Fig. 1). The inner bay has a mean depth of 5 m, is nutrient-rich, and is heavily influenced by inputs from the Saginaw River. Prior to heavy infestation by *D. polymorpha* in 1991 (Nalepa et al., 1995), the inner bay had some of the highest recorded standing stocks of phytoplankton and productivity in the Great Lakes (Vollenweider et al., 1974). The outer bay has a mean depth of 13.7 m, and is more influenced by the colder, nutrient-poor waters of Lake Huron. We collected samples at two sites, one in the

inner bay, and one in the outer bay (Fig. 1). The inner bay site is Station 5, and the outer bay site is Station 19, as designated in previous papers (Fahnenstiel et al., 1995; Johengen et al., 1995). Water depths were 3 m and 3.7 m at the two sites, respectively.

Field and laboratory procedures

D. polymorpha was collected from the two sites on a monthly basis from April through November in 1995 and 1996. Because of poor weather conditions, both sites were not always sampled each month. Rocks with attached mussels were hand collected by divers, placed in coolers and covered with damp paper towels for transport back to the laboratory. Mussels 10–20 mm in shell length from each site were promptly (within 1 day of collection) placed in liquid nitrogen and stored until ETS could be analyzed. For determination of respiration rates, mussels of similar size (10–20 mm) were placed into ambient water and kept at ambient temperatures for 12–16 h prior to rate measurements. During this acclimation period, the water was renewed such that particle concentrations did not decline below 50% of the concentration found under *in situ* conditions. In 1995, individual mussels were placed into each of six 60 ml-BOD bottles and incubated at ambient temperature for 4–5 h. BOD bottles containing only site water were used for initial oxygen concentrations and as controls. Initial and final oxygen concentrations were determined using the micro-winkler method. After the experimental period, the animals were shucked and dry weights determined by placing individuals into pre-weighed aluminum boats, dried at 60 °C for 48 h, and weighed on a Cahn electro balance (± 0.01 mg). In 1996, three mussels were placed into each of nine replicate BOD bottles for determination of respiration rates. After the experimental period, the animals were shucked, and weights determined. The wet tissue was then stored in liquid nitrogen until ETS analysis. Thus, in 1995 ETS activity and respiration rates were determined on separate mussels collected on the same date, whereas in 1996 ETS and respiration were measured on the same individuals. The shell length of each animal collected in 1995 and 1996 was measured to the nearest 0.5 mm using a calibrated micrometer. Dry weights of mussels collected in 1996 were determined from length-weight relationships derived from mussels collected at the same site on the same sampling date (Nalepa, unpublished data).

ETS activity was determined following the method of Owens & King (1975), where INT-Tetrazolium is reduced to the optically active INT-Formazan when substituted for oxygen as the terminal electron acceptor. All reagents were freshly made within 24 h of each assay and kept refrigerated until used. Also, all tissues and reagents were kept on ice, and all assay procedures were carried out in an ice bath. Tissue samples were removed from liquid nitrogen storage, placed in ETS-B solution (75 mg $mgSO_4$, 1.5 mg ml^{-1} polyvinylpyrrolidone, and 0.2% (v:v) Triton X-100 in 0.1 m phosphate buffer, pH 8.5), and ground in a teflon-glass tissue grinder for three 20 s intervals. The volume of the homogenate was recorded, and triplicate 3 ml subsamples were each placed in centrifuge tubes and centrifuged at 10000 *g* for 20 min. One ml of supernatant was then pipetted off each centrifuge tube into a culture tube to which 3 ml substrate solution (1.2 mg ml^{-1} NADH, 0.2 mg ml^{-1} NADPH in ETS-B solution) and 1 ml INT solution (2 mg ml^{-1} INT-Tetrazolium in double distilled water, pH 8.5) was added. For the mussel samples that were frozen directly, assays were incubated at two different temperatures: ± 1 °C of ambient, and at a constant 25 °C. The latter temperature is the approximate maximum temperature at which oxygen uptake is directly related to temperature before declining with further temperature increases (McMahon, 1996), and is also the maximum *in situ* water temperature recorded in the bay (Table 1). Mussels from the respiration rate determinations in 1996 were only assayed at the ambient temperature on each sampling date. After a 20 min incubation period, the reaction was stopped with 1 ml quench solution (50% formalin, 50% 1 m H_3PO_4). The absorbance of each sample was then measured spectrophotometrically at 490 nm. The absorbance value was corrected by a turbidity blank, which consisted of 4 ml ETS-B and 1 ml quench. ETS was then calculated by the following equation:

$$\text{ETS } \mu g\ O_2\ mg\ DW^{-1}\ hr^{-1} = (A/15.9) \times (60/I) \times ((V \times H)/(S \times M)) \times (32/2), \quad (1)$$

where A is the corrected sample absorbance (cm^{-1}), 15.9 is the molar absorbance for INT-formazan (μmol ml^{-1} cm^{-1}), I is the incubation time (minutes), V is the final reaction volume (ml), H is the total homogenate volume (ml), S is the incubated volume (ml), M is the sample size (mg DW), 32/2 is the conversion of μmol INT-formazan to $\mu g\ O_2$.

Table 1. Temperature, particulate organic carbon (POC), and chlorophyll (CHL) at the inner bay and outer bay sites on sampling dates in 1995 and 1996. Dates with an asterisk are the dates in which ETS and respiration rates were measured. Values for other dates (without an asterisk) are taken from a separate monitoring program and included here to better characterize the two sites

Sampling date	Temperature (°C)		POC (mg l^{-1})		CHL ($\mu g\ l^{-1}$)	
	Inner	Outer	Inner	Outer	Inner	Outer
*24 Apr 95	7.0	7.0	0.71	0.44	2.68	1.15
2 May 95	8.5	6.5	0.75	0.16	3.68	0.78
17 May 95	16.0	13.5	0.32	0.15	0.57	0.33
*25 May 95	16.0	12.0	0.37	0.22	0.61	0.6
12 June 95	19.0	16.0	0.35	0.30	0.84	1.59
*19 Jun 95	20.0	20.0	0.44	0.24	1.69	0.43
*12 Jul 95	24.0	24.0	2.79	1.41	16.10	7.85
17 Jul 95	24.0	20.0	2.82	1.14	13.01	5.50
*15 Aug 95	25.0	25.0	3.09	2.4	9.01	9.42
21 Aug 95	24.0	23.0	2.91	0.62	7.64	2.25
12 Sep 95		18.5	2.07	1.70	3.74	6.18
*18,26 Sep 95	17.0	15.0	3.0	0.95	6.28	6.91
25 Oct 95	10.0	9.0	1.96	0.52	13.92	1.91
*08 Nov 95	5.0		1.58		8.26	
4 May 96		5	0.32	0.14	0.76	0.29
*15, 17 May 96	9.0	8	0.15	0.21	1.36	0.53
28 May 96	14.0	13	0.23	0.10	0.80	0.12
11 Jun 96	17	15	0.28	0.16	0.85	1.03
*12 Jun 96	17	18	0.26	0.25	0.71	0.89
27 Jun 96	23	18.5	0.25	0.41	0.45	1.95
15 Jul 96	22.5	19.5	0.44	0.35	1.85	2.26
*25 Jul 96	22	19	0.5	0.52	3.49	2.15
21 Aug 96	25	23	2.78	1.73	16.79	9.73
*29,30 Aug 96	21	21	2.24	1.73	13.45	2.26
20 Sep 96	18.2	18	1.77	0.16	7.68	0.25
*25 Sep 96	16	16	1.77		16.79	
*13 Nov 96	6				7.68	

As noted, ETS activity and respiration rates were determined on mussels 10–20 mm in shell length. Mean (± SE) shell lengths (mm) of mussels used for determination of respiration rates and ETS were: 1995 respiration = 14.8±0.4 and 15.2±0.6 for the inner and outer bay, respectively; 1995 ETS = 14.3±0.3 and 14.5±0.3; 1996 respiration and ETS = 13.2±0.6 and 14.6±0.8.

Water was collected at 1 m below the surface at each site for determination of temperature, particulate organic carbon (POC), and chlorophyll (CHL) on each date mussels were collected. Additional data on temperature, POC and CHL, collected on other dates as part of a separate monitoring program, were also used to further characterize the two sites (Nalepa, unpublished data). POC was measured using a Perkin Elmer (model 2400) CHN elemental analyzer, and CHL was measured using the methods of Strickland & Parsons (1972). Further details of analytical methods are given in Nalepa et al. (1996).

Results

Site characteristics

Water temperature, POC and CHL at the two sites on each sampling date as well as additional data from a separate monitoring program are given in Table 1. Mean temperature was higher in the inner bay than the outer bay; in 1995 mean temperatures were 17.5 and 15.9°C, respectively (paired *t*-test, $P < 0.005$), and in 1996 mean temperatures were 18.6 and 17.2°C (paired *t*-test, $P < 0.05$). Mean POC at the inner and outer bay sites in 1995 was 1.66 and 0.78 mg l^{-1}, respectively (paired *t*-test, $P < 0.005$) and in 1996 was 0.84 and 0.52 mg l^{-1}, respectively (paired *t*-test, $P = 0.09$); mean chlorophyll in 1995 was 6.13 and 3.45 mg l^{-1} (paired *t*-test, $P < 0.05$), and in 1996 was 4.38 and 1.95 mg l^{-1} (paired *t*-test, $P = 0.08$). Greatest differences between the two sites occurred in late summer of both years when large blooms of the cyanophyte *Microcystis* occurred in the inner bay, but occurred to a much lesser extent in the outer bay (Vanderploeg, NOAA Great Lakes Environmental Research Lab, unpublished data). Water columns at both sites are well-mixed, and oxygen concentrations are near saturation throughout the year (Nalepa et al., 1996).

Densities of *D. polymorpha* were 17 776 m^{-2} in 1995 and 19 349 m^{-2} in 1996 at the outer bay site, and 1018 m^{-2} in 1995 and 3067 m^{-2} in 1996 at the inner bay site (Nalepa, unpublished data). The difference in density between the sites can be attributed to differences in the amount of hard substrate. The substrate at the outer bay site consisted mostly of slabs of bedrock and large cobble, while the substrate at the inner bay site consisted of some cobble scattered on sand.

ETS Activity

At ambient temperatures, ETS activity ranged from 2–40 $\mu g\ O_2$ mg $DW^{-1}\ h^{-1}$ over the 2-year period. Values at the two sites increased with temperature to

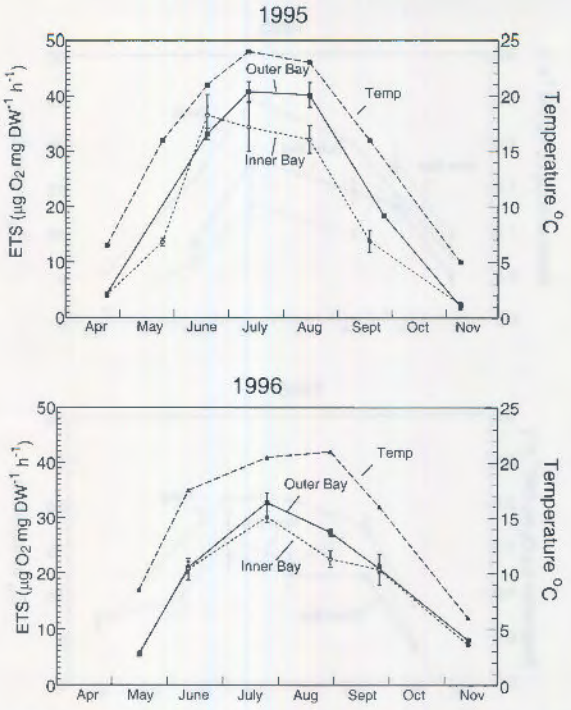

Figure 2. Mean (± SE) ETS activity in *D. polymorpha* from Saginaw Bay at ambient assay temperatures, 1995 and 1996. Inner bay: open circles, outer bay: solid squares.

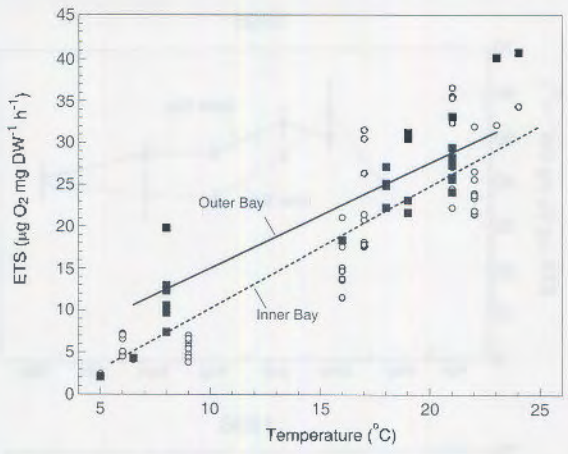

Figure 3. Relationship between ETS (μg O_2 mg DW $^{-1}$ h^{-1}) and temperature (T, °C) for all sampling dates in 1995 and 1996. Inner bay regression: ETS = 1.457 (T) − 4.329 (r^2= 0.76, $P <$ 0.001); outer bay regression: ETS = 1.257 (T) + 2.554 (r^2 = 0.72, $P < 0.001$). Intercepts were significantly different, but slopes were similar ($p = 0.31$). Inner bay: open circles, outer bay: solid squares.

maximum values between early June and August, and then declined in the fall of both years (Fig. 2). During the summer, ETS activity tended to be higher at the outer bay site, although there was no significant difference between the sites when all sampling dates were considered; inner and outer bay means were 19.2 and 21.2 μg O_2 mg DW^{-1} h^{-1} (P = 0.06; paired t-test). For all sampling dates, there was a strong, direct relationship between ETS activity and temperature (T) at both of the sites (Fig. 3). Linear regression equations were: ETS = 1.457∗T − 4.329 (r^2=0.76) at the inner bay site, and ETS = 1.257∗T + 2.544 (r^2 = 0.72) at the outer bay site. Based on ANCOVA, slopes were similar (P = 0.31) but intercepts were significantly different ($P < 0.04$), indicating that ETS response to temperature was similar at the two sites but, for a given temperature, ETS was higher at the outer bay site. Based on these regressions, the Q_{10} (10–20 °C) was 2.4 and 1.8 at the inner and outer bay sites, respectively.

In addition to conducting assays at ambient temperatures, we also conducted assays at a constant temperature (25 °C) on each sampling date. By keeping temperature constant, these assays determined if other variables besides temperature were contributing to seasonal changes in ETS activity. Although changes were not as pronounced as found for assays at ambient temperatures, there was a seasonal pattern in both years, with highest values occurring in June and July (Fig. 4). Also, there was a more consistent difference in ETS activity between the two sites. These ETS values were significantly higher at the outer bay site compared to the inner bay site over the 2-year period (paired t-test; P = 0.01). ETS was higher at the outer bay site on 9 of the 11 sampling dates when both sites were sampled.

Respiration rates varied from 0.2 to 1.7 μg O_2 mg DW^{-1} h^{-1} over the 2-year period (Fig. 5). At the outer bay site, seasonal patterns in respiration rates were generally similar to those found for ETS; that is, rates increased to maximums in summer and then declined through the fall. Rates at the inner bay site, however, were more inconsistent. Rates increased to a maximum in late spring, declined in mid summer, increased somewhat in late summer, and then declined through fall. As found for ETS activity, respiration rates (R) increased with temperature at both sites (Fig. 6), however, the relationship was much more variable at the inner bay site. The relationships were: R = 0.056∗T +0.284 (r^2 = 0.27) at the inner bay site, and R = 0.078∗T − 0.215 (r^2 = 0.88) at the outer bay site. The two regressions were not significantly different (ANCOVA; $P > 0.05$). Q_{10} (10–20 °C) values for

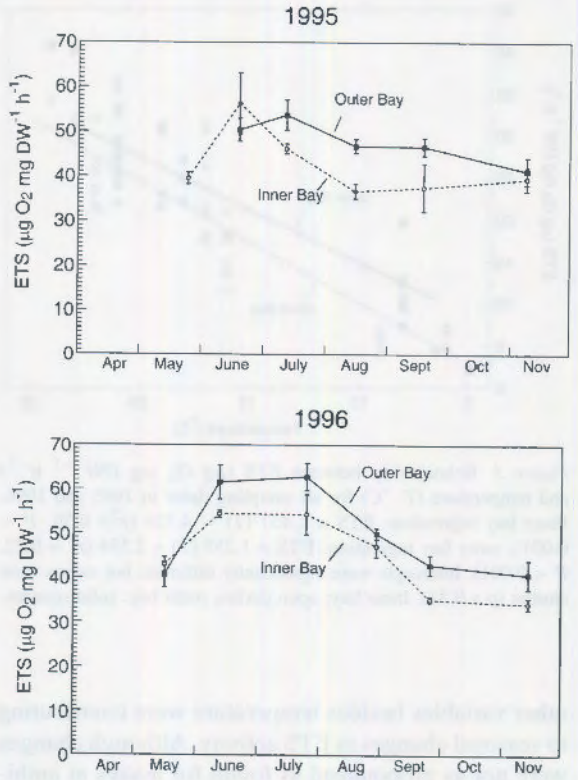

Figure 4. Mean (± SE) ETS activity in *D. polymorpha* from Saginaw Bay at a constant assay temperature of 25 °C on each sampling date, 1995 and 1996. Inner bay: open circles, outer bay: solid squares.

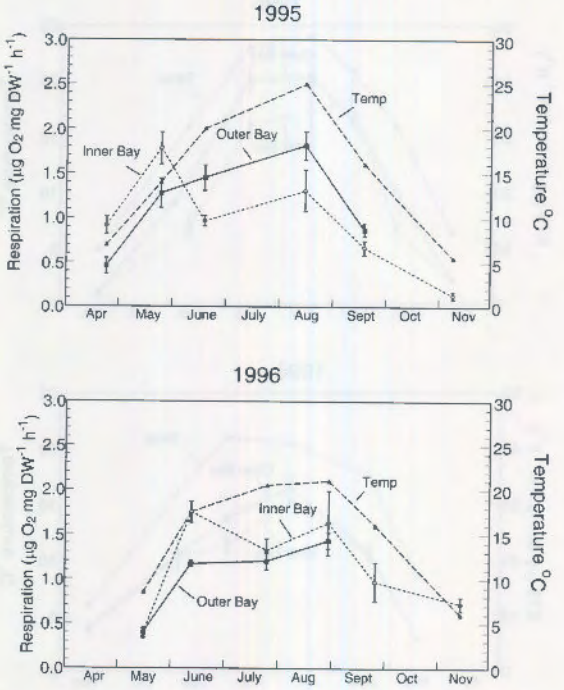

Figure 5. Mean (± SE) respiration rates in *D. polymorpha* form Saginaw Bay , 1995 and 1996. Inner bay: open circles, outer bay: solid squares.

respiration were 1.7 and 2.4 at the inner and outer bay sites, respectively.

Since ETS measures potential metabolic activity and respiration measures actual activity, the ratio (R:ETS) provides an indication of the proportion of the enzymatic system that is actually utilized, and the variability of this ratio defines the utility of ETS in estimating actual metabolic activity. Despite fewer values in 1995 compared to 1996, yearly patterns were the same for the two sites. In both years, there was a direct correlation between respiration and ETS activity (Fig. 7), however, the ratio was more variable at the inner bay site. Correlation coefficients between ETS and respiration in 1995 and 1996 were 0.38 and 0.54 at the inner bay site, and 0.99 and 0.86 at the outer bay site. The greater variability in the ratio at the inner bay site can be attributed to wide fluctuations in respiration rates relative to ETS over a seasonal period (compare Figs 3 and 6). Mean monthly ratios ranged between 0.02 and 0.22, and annual means ranged between 0.04 and 0.09 at both sites. Ratios were significantly higher at the inner bay site in 1996 ($P < 0.05$), but the difference was not significant in 1995. The linear regressions of the ratios at the two sites were significantly different from each other (ANCOVA: intercept, $P < 0.001$; slope, $P < 0.001$); ratios decreased with temperature at the inner bay site, but increased only slightly with temperature at the outer bay site (Fig. 8).

Discussion

Since ETS integrates metabolic activity over a several week period prior to the actual measurement, and is less subject to short-term fluctuations during the measurement process, it has been suggested that ETS is a more useful indicator of *in situ* metabolism than respiration rates in benthic macroinvertebrates (Cammen et al., 1990). Yet, because ETS measures metabolic activity as potential oxygen consumption, while respiration rates measure actual consumption, the relationship between these two variables, and factors that affect this relationship, must be clearly understood before ETS can be widely applied when defining energy budgets for a specific population.

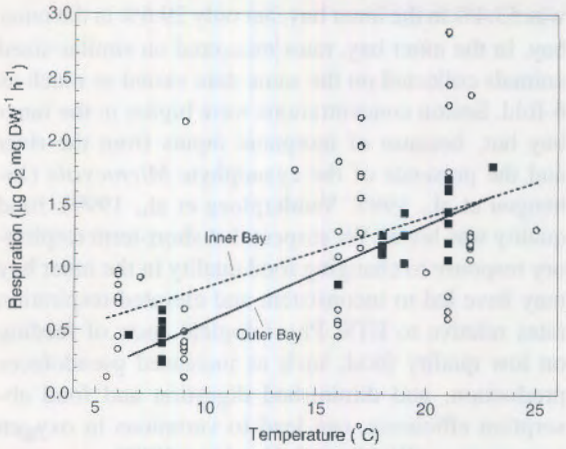

Figure 6. Relationship between respiration rates (R, μg O_2 mg DW^{-1} h^{-1}) and temperature (T, °C) for all sampling dates in 1995 and 1996. Inner bay regression: $R = 0.056\ (T) + 0.284$ ($r^2 = 0.27$, $P < 0.001$); outer bay regression: $R = 0.078\ (T) - 0.215$ ($r^2 = 0.88$, $P < 0.001$). Intercepts and slopes were not significantly different ($P > 0.10$). Inner bay: open circles, outer bay: solid squares.

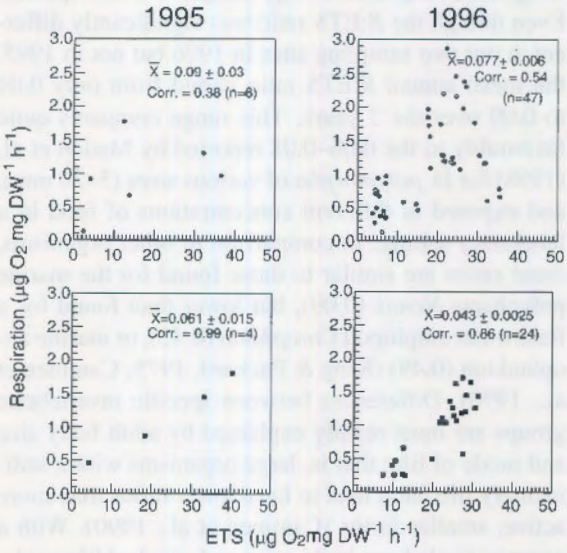

Figure 7. Relationship between respiration rates (R) and ETS (R/ETS ratio) in *D. polymorpha*, 1995 and 1996. Inner bay: upper row, outer bay: lower row.

Over the 2-year sampling period, we found that both ETS activity and respiration rates were significantly related to temperature at both sampling sites. While the response of ETS activity to seasonal temperature changes has not been previously examined in *D. polymorpha*, our finding of a seasonal correlation between oxygen consumption and temperature compares to similar findings by Quigley et al.

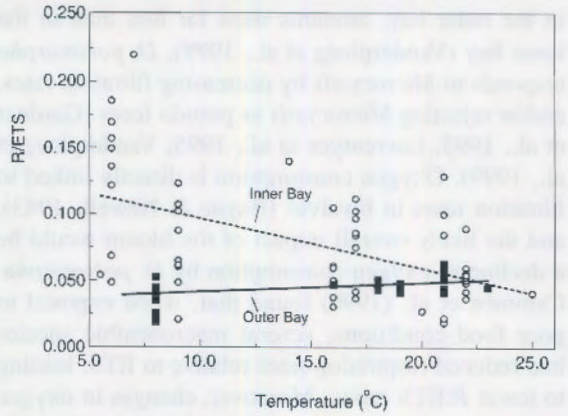

Figure 8. Relationship between respiration rates (R) and ETS (R/ETS ratio) and temperature (T, °C) for all sampling dates in 1995 and 1996. Inner bay regression: $R/\text{ETS} = -0.004\ (T) + 0.134$ ($r^2 = 0.26$, $P < 0.001$); outer bay regression: $R/\text{ETS} = 0.001\ (T) + 0.021$ ($r^2 = 0.49$, $P < 0.001$). Intercepts and slopes were significantly different (ANCOVA; $P < 0.001$). Inner bay: open circles, outer bay: solid squares.

(1993) and Sprung (1995c), and is consistent with laboratory studies (Woynarovich, 1961). On the other hand, Stoeckmann & Garton (1997) found that oxygen consumption and temperature were not related on a seasonal basis. These authors attributed the lack of correlation to an ability of *D. polymorpha* to adjust metabolic activity within normal summer temperature patterns, but such an acclimation pattern was not apparent in our data. Q_{10} values (10–20 °C) for both ETS and respiration ranged from 1.6 to 2.5 and were within the range of values reported for *D. polymorpha* by others (for summary see McMahon, 1996).

Based on our derived seasonal relationships, the effect of temperature change was greater for ETS than for respiration, therefore the R:ETS ratio also varied with temperature at both sites. A similar temperature-dependence of the R:ETS ratio has been found in lake plankton (Del Giorgio, 1992) and in individual zooplankton (James, 1987). However, the response of ETS and respiration to temperature changes was different for the two sites, and thus the ratios were site specific. The ratio decreased with increased temperature at the inner bay site, and increased slightly with temperature at the outer bay site. The reason for this varying response relative to temperature is not clear, but we suggest that differences in food quality played a role. In late summer 1995 and 1996 when temperatures were at a maximum, a bloom of the toxic cyanophyte *Microcystis* occurred in the inner bay. Although some *Microcystis* was also found

in the outer bay, amounts were far less than in the inner bay (Vanderploeg et al., 1999). *D. polymorpha* responds to *Microcystis* by decreasing filtration rates, and/or rejecting *Microcystis* as psendo feces (Gardner et al., 1995; Lavrentyev et al., 1995; Vanderploeg et al., 1999). Oxygen consumption is directly linked to filtration rates in bivalves (Bayne & Newell, 1983), and the likely overall impact of the bloom would be a decline in oxygen consumption by *D. polymorpha*. Cammen et al. (1990) found that, when exposed to poor food conditions, several macrobenthic species had reduced respiration rates relative to ETS, leading to lower *R*:ETS ratios. Moreover, changes in oxygen consumption relative to food conditions in *D. polymorpha* are most pronounced at higher temperatures (Alexander, 1994). In the outer bay, an increase in respiration relative to ETS may be expected at higher summer temperatures as short-term demands for oxygen must meet increased metabolic costs at a given food level.

The influence of other factors on ETS activity besides temperature was apparent when assays were conducted at a constant temperature; ETS increased to a maximum in late spring and then declined. In late spring, filtration rates of *D. polymorpha* were at a seasonal maximum in both the inner and outer bay (Fanslow et al., 1995). Also, gonad volume was at a peak in the late spring period prior to spawning (Nalepa, unpublished data), and reproductive activity can increase oxygen consumption (Lyashenko & Karchenko, 1989; Sprung, 1995c). Stoeckman & Garton (1997) reported that the greatest fluctuations in metabolic costs occurred in May and June when Lake Erie mussels were actively undergoing gametogenesis.

ETS activity was generally higher in mussels from the outer bay, but consistent differences in respiration rates between the two sites were not apparent. As a result, *R*:ETS ratios were lower in the outer bay on most sampling dates. Because of lower seston concentrations, filtration rates of *D. polymorpha* were higher in the outer bay compared to the inner bay (Fanslow et al., 1995), and likely accounts for the higher ETS activity. Since ETS and respiration rates should theoretically adjust over time such that the ratio would be similar at both sites, the question arises as to why respiration rates were not higher relative to ETS in the outer bay or, conversely, why respiration rates were not lower in the inner bay. Respiration rates were highly variable in the inner bay; mean coefficients of variation for the *R*:ETS ratio, as calculated in 1996 (both *R* and ETS were measured on the same animals) was 53.4% in the inner bay, but only 29.6% in the outer bay. In the inner bay, rates measured on similar-sized animals collected on the same date varied as much as 6-fold. Seston concentrations were higher in the inner bay but, because of inorganic inputs from the river and the presence of the cyanophyte *Microcystis* (Johengen et al., 1995; Vanderploeg et al., 1999), food quality was lower. We suspect that short-term respiratory response to changing food quality in the inner bay may have led to inconsistent and elevated respiration rates relative to ETS. Physiological costs of feeding on low quality food, such as increased pseudofeces production, and diminished digestion and food absorption efficiency, can lead to variations in oxygen consumption (Widdows & Hawkins, 1989).

Our results indicate that ETS activity provided a less variable measure of metabolic activity than respiration rates in *D. polymorpha* over a seasonal period. Yet the consistency of the relationship between respiration and ETS is critical if ETS activity is to be used in integrated, long-term energy budgets for this species. Even though the *R*:ETS ratio was significantly different at our two sampling sites in 1996 but not in 1995, the mean annual *R*:ETS ratio varied from only 0.04 to 0.09 over the 2 years. This range compares quite favourably to the 0.06–0.08 reported by Madon et al. (1998) for *D. polymorpha* of various sizes (5–30 mm), and exposed to different concentrations of food in a laboratory setting. In comparison to other organisms, these ratios are similar to those found for the marine polychaete *Nereis* (0.09), but lower than found for a freshwater amphipod *Corophium* (0.42), or marine zooplankton (0.49) (King & Packard, 1975; Cammen et al., 1990). Differences between specific invertebrate groups are most readily explained by adult body size and mode of life; that is, large organisms with a sedimentary life habit tend to have lower ratios than more active, smaller forms (Cammen et al., 1990). With a comparatively large body mass and attached life mode, the low ratio found for *D. polymorpha* may be expected. In organisms with low ratios, the capacity for elevated metabolism is maintained, even though activity is limited. Filtration rates in *D. polymorpha* can vary widely on a monthly basis (Fanslow et al., 1995), and maintaining the enzyme 'machinery' for increased metabolic activity would be an advantage. Besides having comparable *R*:ETS ratios, total ETS activity was also similar for *D. polymorpha* and *Nereis*. ETS activity in Nereis was 10–13 μg O_2 mg DW^{-1} h^{-1} over a seasonal period at a response temperature of 10 °C (Cammen et al., 1990). From our derived

relationships between ETS and temperature over a seasonal period, ETS in *D. polymorpha* was 15.1 μg O_2 mg DW^{-1} h^{-1} at the outer bay site and 10.2 μg O_2 mg DW^{-1} h^{-1} at the inner bay site at a temperature of 10 °C.

In summary, we found that ETS activity in *D. polymorpha* provided a less variable estimate of metabolic activity than respiration rates over a broad range of food and temperature conditions. Spatial differences in ETS activity and *R*:ETS ratios can best be explained by differences in filtration rates and other metabolic processes affected by food quantity and quality. While ratios were site specific, the range in mean annual ratios was minimal. Subsequently, the measurement of ETS may prove useful in estimating oxygen consumption for broad-based bioenergetics models (Madenjian, 1995) or assessments of oxygen depletion in specific systems (Effler & Siegfried, 1994).

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